

A Phylogenetic Analysis of the Superfamily Platanistoidea (Mammalia, Cetacea, Odontoceti)

by

Lawrence G. BARNES*)

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Abstract

The family Platanistidae includes fossil and Recent dolphin-like toothed cetaceans. Living platanistids of the genus *Platanista* WAGLER, 1830, called Ganges and Indus River dolphins, or susus, live in fresh waters of southeast Asia. Fossil platanistids are known only from Miocene near shore marine and fresh water deposits in the Northern Hemisphere. The most primitive named platanistid is *Prepomatodelphis korneuburgensis* BARNES, 2002, a long-snouted species of latest Early Miocene age (Karpatian age, late Burdigalian correlative) from the Korneuburg Formation, in the Korneuburg Basin, which was an estuary of the ancient Vienna Basin, Austria. The morphology of *P. korneuburgensis* helps determine character polarity among the Platanistidae and related cetaceans in the superfamily Platanistoidea. A cladistic analysis of fossil and living Platanistoidea supports theories of monophyly of the superfamily Platanistoidea and of the family Platanistidae. Two subfamilies of the Platanistidae are the Pomatodelphininae and Platanistinae. The Pomatodelphininae includes species of the genera *Prepomatodelphis* BARNES, 2002, *Zarhachis* COPE, 1868 (Middle Miocene of Maryland), and *Pomatodelphis* ALLEN, 1921 (Middle and Late Miocene of France, Florida, and Alabama), all of which have a dorsoventrally flattened rostrum and symphyseal portion of the mandible. The Platanistinae includes platanistids with an anteroposteriorly lengthened zygomatic process of the squamosal, transversely flattened rostrum and symphyseal portion of the mandible, and an enlarged supraorbital maxillary crest that is invaded by the pterygoid air sinus. An apparent platanistine occurs in the Early Miocene Nye Formation in Oregon, U.S.A. A new extinct odontocete family, the Allodelphinidae, includes long-snouted stem platanistoids of the genus *Allodelphis* WILSON, 1935, and some related Miocene species in the North Pacific realm. The Allodel-

phinidae have primitive cranial characters, and their long rostra and mandibles appear to have evolved convergently with the Pomatodelphininae.

Keywords: Cetacea, Platanistoidea, Platanistidae, Pomatodelphininae, Platanistinae, Allodelphinidae, systematics, Korneuburg Basin, Austria, Miocene

Zusammenfassung

Die Familie der Platanistidae umfaßt die fossilen und rezenten Vertreter delphinähnlich bezahnter Wale. Rezente Vertreter des Genus *Platanista* WAGLER, 1830, die sog. Ganges- und Indus-Delphine, auch susus genannt, leben im Süßwasser Südost-Asiens. Fossile Platanistiden kennt man nur aus dem Miozän in Küsten- und Süßwassersedimenten der nördlichen Hemisphäre. Der älteste bekannte Platanistide ist *Prepomatodelphis korneuburgensis* BARNES, 2002, eine langschnauzige Art aus dem obersten Untermiozän (Karpas, entspricht dem oberen Burdigal) aus der Korneuburg Formation des Korneuburger Beckens, einem Ästuar des ehemaligen Wiener Beckens in Österreich. Die Morphologie von *P. korneuburgensis* hilft bei der Bestimmung der Polarität der Merkmale innerhalb der Platanistidae und verwandter Wale der Überfamilie Platanistoidea. Eine cladistische Analyse der fossilen und lebenden Platanistoidea unterstützt die Hypothese der Monophylie der Platanistoidea und Platanistidae. Man unterscheidet innerhalb der Platanistidae zwei Unterfamilien: die Pomatodelphininae und die Platanistinae. Die Pomatodelphininae umfassen die Genera *Prepomatodelphis* BARNES, 2002, *Zarhachis* COPE, 1868 (Mittelmiozän von Maryland), und *Pomatodelphis* ALLEN, 1921 (Mittel- und Obermiozän von Frankreich, Florida und Alabama). Die Pomatodelphininae haben ein dorsoventral abgeflachtes Rostrum und eine ebensolche Symphysenregion der Mandibula. Die Platanistinae haben eine anterioposterior verlängerten Processus zygomaticus am Squamosum, ein seitlich abgeplattetes Rostrum und Symphysenregion der Mandibula sowie eine vergrößerte, supraorbital gelegene Crista am Maxillare, die eine Sinusbildung enthält. Ein augenscheinlicher Platanistine kommt in der untermiozänen Nye Formation in Oregon (U.S.A.) auf. Eine neue, ebenfalls

*) Dr. Lawrence G. BARNES, Curator of Vertebrate Paleontology, Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007, U.S.A.

ausgestorbene Familie der Zahnwale, die Allodelphinidae, umfaßt langschnauzige basale Platanistoiden der Gattung *Allodelphis* WILSON, 1935 und einige verwandte miozäne Arten aus dem nordpazifischen Raum. Die Allodelphinidae haben primitive Schädelmerkmale, ihre langen Rostren und Mandiblen dürften sich wohl konvergent zu denen der Pomatodelphininae entwickelt haben.

1. Introduction

Among the Odontoceti, or echolocating toothed whales, species of the superfamily Platanistoidea constitute an early adaptive radiation that flourished, then subsequently declined and was replaced by other odontocete groups. The superfamily, first established by SIMPSON (1945), has a complex history in cetacean taxonomic studies. In several previous classifications (e.g. SIMPSON, 1945), it included other so-called "river dolphins" of the families Iniidae, Lipotidae, or Pontoporiidae, animals that are now generally classified in other superfamilies (McKENNA & BELL, 1997:386-387).

The current concept of the superfamily Platanistoidea has become dramatically altered (MUIZON, 1985, 1987, 1990, 1994; FORDYCE, 1994) with the inclusion of the Late Oligocene to Middle Miocene "shark-toothed" whales of the family Squalodontidae (MUIZON, 1994; FORDYCE, 1994), of archaic Late Oligocene dolphin-like members of the family Waipatiidae (FORDYCE, 1994), of more derived Miocene dolphin-like species of the family Squalodelphinidae (MUIZON, 1987; FORDYCE, 1994), and with a more restricted use of the family Platanistidae (FORDYCE, 1994; BARNES, 2002). Today only the family Platanistidae survives, represented by relict fresh water dolphins of the genus *Platanista* WAGLER, 1830.

The long-snouted fossil dolphin, *Prepomatodelphis korneuburgensis* BARNES, 2002, is the earliest-occurring and most primitive recognized platanistid. It is known only by its holotype, from the latest Early Miocene age (Karpatian stage, late Burdigalian correlative) marine Korneuburg Formation of the Korneuburg Basin, Austria. The Korneuburg Basin was a small estuary that was connected in Miocene time to the larger Vienna Basin.

The purpose of this paper is to provide a phylogenetic analysis of the Platanistoidea. A poorly known earliest Miocene odontocete from central California, U.S.A., *Allodelphis pratti* WILSON, 1935, is a very primitive platanistoid. Illustrations are presented here of the holotypes of *A. pratti* and *P. korneuburgensis* to demonstrate some of the characters that were used in the pylogenetic analysis.

2. Material and Methods

2.1. Institutional abbreviations

AMNH Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York, U.S.A.

ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
 CAS Division of Birds and Mammals, California Academy of Sciences, San Francisco, California, U.S.A.
 ChM Charleston Museum, Charleston, South Carolina, U.S.A.
 LACM Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
 MCZ Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts, U. S. A.
 NHMW Naturhistorisches Museum Wien, Vienna, Austria.
 UCMP Museum of Paleontology, University of California, Berkeley, California, U. S. A.
 UMMP Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U. S. A.
 USNM Departments of Paleobiology and Mammalogy, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U. S. A.
 YPM Peabody Museum, Yale University, New Haven, Connecticut, U. S. A.

2.2. Specimens and resources consulted

Zygorhiza kochii (REICHENBACH, 1847). A referred specimen, USNM 11962, from the Late Eocene age Jackson Group in Alabama, U.S.A., was supplemented by text and illustrations that were provided by KELLOGG (1936).

Agorophius pygmaeus (MÜLLER, 1849). The holotype partial cranium was probably derived from the Late Oligocene age Cooper Marl near Charleston, South Carolina, U.S.A., and is now lost or misplaced (WHITMORE & SANDERS, 1977: 308-309). Characters for this species were determined from text and illustrations that were provided by TRUE (1907), WHITMORE & SANDERS (1977:308-309, fig. 1b), FORDYCE (1981), and MUIZON (1994: fig. 5d), and from a more recently-obtained cranium (ChM specimen, replica LACM 143475) of Late Oligocene age from South Carolina, U.S.A., that appears to represent this species.

Allodelphis pratti WILSON, 1935. The holotype, YPM 13408 (Figs. 1-3 herein), includes the cranium (lacking the rostrum), with broken parts of the right dentary adhering to both the dorsal and ventral sides of the right supraorbital process, the right petrosal (which has been removed from the cranium), and the atlas vertebra (which still adheres to the occipital condyles). A right humerus was incorrectly catalogued with this specimen, but is from a different individual, probably some species of Eurhinodelphinidae. The correct humerus of *A. pratti* is demonstrated by a referred specimen of the same species, UCMP 83791, that was excavated near the type locality. UCMP 83791 also includes the left tympanic bulla, the atlas and two other cervical vertebrae, four thoracic vertebrae, several ribs, the manubrium, and the left humerus and left ulna (which are fused together at the elbow joint). Another specimen, USNM 13673, possibly represents *A. pratti*, is definitely assignable to the genus *Allodelphis*, and includes a crushed and broken cranium and mandible, and associated vertebrae, ribs, and forelimb bones. It confirms the rostral morphology of this genus. All three of these

specimens are from the Woody Local Fauna (characterized by MITCHELL & TEDFORD, 1973), and were collected from a limited geographic area southwest of Woody, a small town that is northeast of Bakersfield in Kern County, California, U.S.A. These specimens are from a near-shore marine deposit that is mapped as the undifferentiated Freeman Silt and Jewett Sand, is earliest Miocene in age, and has been correlated with the Vaqueros marine invertebrate stage and the Arikarean North American Land Mammal Age (see BARNES, 1977:324-325, table 2).

***Squalodon calvertensis* KELLOGG, 1923.** Observations were made on the holotype, USNM 10484, and referred specimen, USNM 206288, both of Middle Miocene age from the Calvert Formation, Calvert County, Maryland, U.S.A. (see KELLOGG, 1923; DOOLEY, 2005).

***Waipatia maerewhenua* FORDYCE, 1994.** The holotype and only known specimen is of Late Oligocene age from New Zealand, and its characters were illustrated and described by FORDYCE (1994).

***Notocetus vanbenedeni* MORENO, 1892.** Images of the holotype, in the La Plata Museum, Argentina, are in LYDEKKER (1894). A referred specimen, AMNH 9485, was described by TRUE (1910; and see MUIZON, 1987; FORDYCE, 1994).

***Prepomatodelphis korneuburgensis* BARNES, 2002.** The holotype and only known specimen is NHMW 2002z0001/0000 (Figs. 4-6 herein), a cranium that lacks part of the left side of the braincase and rostrum, that was collected by Dr. Reinhard Roetzel (Geologische Bundesanstalt Wien) and Dr. Wolfgang Sovis, 22nd October 1989. In the new illustrations presented here, the braincase is shown without the rostrum, from which it has separated because of natural breakage. The two parts can be easily re-attached, and the rostrum was illustrated by BARNES (2002).

The type locality of this species is listed as Teiritzberg 001/I/1-2-3-4/1989, at the community of Teiritzberg, near Korneuburg, in the Korneuburg Basin, Austria. The locality is shown as 001/I on the map that was provided by SOVIS (1998: fig. 3), and is in a stratigraphic section of Miocene marine sediment that was exposed near Am Teiritzberg, which is near Teiritzberg. The location of Teiritzberg is also shown on the geologic map of the Korneuburg Basin that was provided by WESSELY (1998: fig. 4), and the location of the Early Miocene Korneuburg Basin is shown on a regional map that was provided by WESSELY (1998: fig. 1). The source deposit is the Korneuburg Formation (Korneuburger Schichten, see WESSELY, 1998:9, 11, 12, fig. 2), which is correlated with the Karpatian Stage of Central and Western Paratethys, with the late part of the Burdigalian stage of the Mediterranean area, with the NN4 Calcareous Nannoplankton zone, with the MN5 European mammal zone, is latest Early Miocene in age and between approximately 16.5 Ma and 16.7 Ma (HARZHAUSER et al. 2002:441, fig. 1; WESSELY, 1998: fig. 6).

***Zarhachis flagellator* COPE, 1868.** The holotype of *Zarhachis flagellator* is a caudal vertebra (ANSP 11231) from the Calvert Formation in Maryland. Determination of more definitive characters of the species relies on USNM 10485, a partial skeleton, including the rostral portion of a skull

and a petrosal, that was referred to this species by KELLOGG (1924). Details of the cranium are based on USNM 10911, another partial skull that was subsequently described by KELLOGG (1926; and see MUIZON, 1994: fig. 5d); and on USNM 13768, an unpublished referred specimen of the same species. All of these specimens are from the upper part of the Calvert Formation in Maryland, U.S.A., and are of middle Middle Miocene age (GOTTFRIED et al. 1994: 233), correlative with the Barstovian North American Land Mammal Age, approximately 13 Ma to 15 Ma.

***Pomatodelphis stenorhynchus* (HOLL, 1829).** The holotype (in some publications referred to and illustrated under the junior synonym *Delphinus renovi* LAURILLARD, 1844) is the proximal part of a rostrum with parts of the right maxilla and premaxilla, No. 2228, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle in Paris. It is of Middle Miocene age from Maine-et-Loire, Department de l'Orne, France, (see KELLOGG, 1959:19-20), and was illustrated by CUVIER (1836: pl. 224, fig. 38), GERVAIS (1859: pl. 82, figs. 3, 3a), VAN BENEDEN & GERVAIS (1868-1880: pl. LVII, figs. 9, 9a, 9b), and ALLEN (1921: fig. 1). No other specimens can now be confidently referred to this species.

***Pomatodelphis inaequalis* ALLEN, 1921.** The holotype and referred specimens were described by ALLEN (1921), and a referred specimen (MCZ 4433) was described by KELLOGG (1959). All are from the Lower Bone Valley Formation of Florida, U. S. A., and are of late Middle Miocene age, approximately 10.5 Ma to 11.5 Ma, correlative with the early part of the Clarendonian North American Land Mammal Age (MORGAN, 1994:251-252). This is the type species of *Pomatodelphis* ALLEN, 1921.

***Pomatodelphis bobengi* (CASE, 1934).** The holotype (UMMP 15117) is from the same deposits as the specimens mentioned above of *Pomatodelphis inaequalis*, being also from the Lower Bone Valley Formation of Florida, U.S.A., and is of late Middle Miocene age, approximately 10.5 Ma to 11.5 Ma, correlative with the early part of the Clarendonian North American Land Mammal Age (MORGAN, 1994:251-252).

Platanistinae, genus and species undetermined. LACM 131112, section of the symphysis of a mandible (Fig. 7), from LACM locality 5919, in the Early Miocene Nye Formation that is exposed at Holiday Beach, ¼ mile north of the mouth of Thiel Creek, Lincoln County, on the coast of Oregon, U.S.A.; collected by Ms. Wendy Orson, March 1990.

***Platanista gangetica* (ROXBURGH, 1801).** Observations were made of Recent specimens: CAS 16340, a cranium, mandible, and skeleton of an adult female individual from Sind, Pakistan; and USNM 172409; and from illustrations of specimens that have been presented by VAN BENEDEN & GERVAIS (1868-1880), FRASER & PURVES (1960), KELLOGG (1924), PILLERI (1975:188-189), and MUIZON (1994: fig. 6b).

Abbreviations in figures:

Anatomical structures in the illustrations are labeled according to the following abbreviations:

bc – basioccipital crest
 Boc – basioccipital bone
 fmxp – posterior maxillary foramen
 Fr – frontal bone
 gf – glenoid fossa
 lc – lambdoidal crest
 Me – mesethmoid bone
 mrg – mesorostral groove
 ms – tympano-squamosal recess, or fossa for the middle sinus
 Mx – maxillary bone
 Na – nasal bone
 n – narial passage
 nc – nuchal crest
 occ – occipital condyle
 Pa – parietal bone
 pgl – postglenoid process
 Pmx – premaxillary bone
 pmxsf – premaxillary sac fossa
 pop – paroccipital process
 pos – fossa for posterior sinus
 ps – posterolateral sulcus
 Pt(II) – lateral lamina of the pterygoid bone
 pts – fossa for pterygoid sinus
 sop – supraorbital process
 Sq – squamosal bone
 Vo – vomer bone
 zp – zygomatic process of squamosal

In addition to the anatomical abbreviations that identify structures of the holotypes of *Allodelphis pratti* and *Prepomatodelphis korneuburgensis* in Figures 1-6, some of the characters are indicated on these same figures by their numbers from Appendix A, and these are followed by the character states, in parentheses (0 for plesiomorphic, 1 for apomorphic).

2.3. Phylogenetic analysis

The phylogenetic analysis presented here includes 64 characters (Appendix A) that were scored for nine taxa. Only cranial and mandibular characters were used because of the lack of uniform information about postcranial bones for many of the taxa. For example, no postcranial bones are known for *Agorophius pygmaeus*, *Pomatodelphis stenorhynchus*, or *Prepomatodelphis korneuburgensis*. Similarly, although characters of the petrosal and the tympanic bulla are pivotal in recognizing and defining the superfamily Platanistoidea (sensu MUIZON, 1994; FORDYCE, 1994) and the family Platanistidae (sensu BARNES, 2002), because these bones are not included with the holotype and only known specimen of *P. korneuburgensis*, their characters were with one exception (anterior bullar spine) omitted from this analysis.

FORDYCE (1994) prepared a character list and phylogenetic analysis for the superfamily Platanistoidea when he described the primitive platanistoid *Waipatia maerewhenua*. I have used many of the characters from that study, some of which are modified, and in the list of characters (Ap-

pendix A) they are identified by his page and character numbers. More recently, GEISLER & SANDERS (2003) presented a phylogenetic analysis of all Cetacea. Several of their characters are used here, and these are also cited in Appendix A by page and character numbers.

Many of the same taxa that were included in the (1994) analysis by FORDYCE are included here. No Mysticeti were included in the analysis. *Zygorhiza* is represented in this analysis by the Late Eocene *Z. kochii*, and this generalized member of the archaeocete family Basilosauridae serves in the present analysis as the out-group. *Agorophius* is represented by the Late Oligocene *A. pygmaeus*, and this stem odontocete, which was not included in the (1994) analysis by FORDYCE, helps to demonstrate the polarity of the characters of Odontoceti. Morphological characters of *Squalodon*, included in the (1994) analysis by FORDYCE, were based on *Squalodon* as reported by MUIZON (1988a, 1988b, 1994), on *S. calvertensis* as reported by KELLOGG (1923), and on *S. calvertensis* and *S. whitmorei* as reported by DOOLEY (2005). *Notocetus* is based on *N. vanbenedeni*, and it serves to represent the characters of *Squalodelphis*, a closely related genus in the family Squalodelphinidae (see MUIZON, 1987). *Zarhachis flagellator* serves to represent the characters of the derived pomatodelphinine platanistid genus *Pomatodelphis*. I did not include in this analysis a Miocene pomatodelphinine platanistid from France, *Pomatodelphis stenorhynchus*, because the holotype of that species is so incomplete that many relevant characters are not preserved for it.

Not included in this analysis is the problematic family Dalpiaziniidae, originally named Dalpiazinidae by MUIZON (1988a), and subsequently emended by MUIZON (1994: fig. 1), which includes only *Dalpiazina ombonii* (LONGHI, 1898). MUIZON (1988a, 1991) suggested it has close relationships with Squalodontidae, but later (MUIZON, 1994:141) he stated it has "... none of the platanistoid synapomorphies "

Also not included in this analysis is the problematic and poorly characterized family Acrodelphinidae (ABEL, 1905; name emended by RICE, 1998). This family has sometimes been discussed in relationship to odontocetes that are now included in the Platanistoidea (BARNES, 1977), but MUIZON (1988a) relegated the family to Odontoceti, incertae sedis, and restricted it to the type species of the type genus, because it was based on non-diagnostic material.

ABEL (1905) based the family Acrodelphinidae on the genus *Acrodelphis* ABEL, 1900. The type species of *Acrodelphis* is *Champsodelphis denticulatus* PROBST, 1886 (see PROBST, 1886:124), and the type material of *C. denticulatus* is four isolated teeth (see PROBST, 1886: pl. III, figs. 18-21; and PILLERI, 1986:36, table 35, pl. 21, figs. 5-7). These four teeth do not necessarily belong to the same species, and such isolated odontocete teeth are not considered to be diagnostic.

All characters in the analysis are binary characters; none are multistate. The plesiomorphic character states were determined by outgroup comparisons with the archaeocete *Zygorhiza kochii* and with the stem odontocete *Agorophius pygmaeus*. The numbers of the characters in Appendix A are the same as those that appear in the Matrix of Character

Codings (Table 1). Some characters that are not preserved on available specimens, and thus not known for a particular taxon, were scored on the matrix as ?. The entries with a ? are treated the same way in PAUP (SWOFFORD, 1993) as are characters that are known to be absent in a taxon, which in Table 1 are indicated by a dash (-). Examples of the latter are character states relating to the premaxillary sac fossa and premaxillary foramen for *Zygorhiza*, because these are structures that never evolved in the Archaeoceti. Figure 9 shows the only tree that was generated by PAUP from a manipulation of the data in Table 1 using MacClade (Version 3.1.1; MADDISON & MADDISON, 1992).

3. Taxonomy and Systematics

Family Platanistidae (GRAY, 1846) GRAY, 1863

Emended diagnosis of family. A family of the odontocete superfamily Platanistoidea having cranium with elongate and narrow rostrum; premaxillae and maxillae both reaching the anterior rostral extremity; premaxillae and maxillae fused distally; anteroposteriorly elongated groove present on the lateral side of the rostrum approximately following the maxilla/premaxilla suture; posterior maxillary foramen positioned very close to the posterior margin of the premaxilla, and in some taxa overhung by the margin of that bone; posterolateral sulcus on premaxilla enlarged and very deep, particularly in its posterior part, where its lateral margin may overhang the sulcus; lateral lamina of the pterygoid bone present and prominent, formed as an outer bony lamina of the pterygoid within the orbit, and extending posteriorly from the palate and contacting the falciform process of the squamosal (also present in Alldelphinidae); zygomatic process of squamosal expanded dorsoventrally, compressed transversely, and having its medial side excavated and concave; fossa for posterior sinus present on the anterior surface of the paroccipital process; peg present on ridge on articular process of petrosal; tympanic bulla with an elongate and pointed anterior spine; tympanic bulla with a thin outer lip that is smoothly over-arching and high relative to the transverse width of the bulla; symphyseal portion of mandible narrow and anteroposteriorly elongated; mandibular symphysis firmly ankylosed; and all teeth single-rooted.

Type genus: *Platanista* WAGLER, 1830

Comments. The monophyly of the Platanistidae is supported by the phylogenetic analysis that is presented here (Fig. 9). The geochronologically earliest named species that is now recognized as being a platanistid is the latest Early Miocene *Prepomatodelphis korneuburgensis*. All known Platanistidae have a highly modified zygomatic process of the squamosal that is compressed transversely and has a concave medial surface. All known fossil and Recent members of the family Platanistidae have an elongate and narrow rostrum and symphyseal portion of the mandible. A long and narrow rostrum apparently has evolved independently in various clades of Odontoceti. It has been previously reported in the families Eurhi-

nodelphinidae, Pontoporiidae, Iniidae, Kentriodontidae, and Delphinidae, and now also in the new family Alldelphinidae (diagnosed in following text). Although an elongate rostrum and mandible have evolved at various times in various odontocete clades, I include this among the diagnostic characters of the family Platanistidae. *Prepomatodelphis korneuburgensis* demonstrates that a supraorbital maxillary crest is not a diagnostic character of the family Platanistidae. A maxillary crest does occur in some of the more derived taxa, and in some of the taxa that have the crest, it is fenestrated by extensions of the supraorbital lobe of the pterygoid sinus.

The family Platanistidae can be divided into the subfamilies Pomatodelphininae and Platanistinae, and these are diagnosed as follows:

Subfamily Pomatodelphininae BARNES, 2002

Emended diagnosis of subfamily. A subfamily of the family Platanistidae that includes animals differing from members of the subfamily Platanistinae by having cranium with dorsoventrally (rather than transversely) flattened rostrum; transversely expanded posterior end of the premaxilla; eye and bony orbit of normal size (not atrophied); nasal bones not reduced in size but wide transversely; nuchal crests enlarged, prominent, and transversely oriented; dorsoventrally (rather than transversely) flattened symphyseal portion of mandible; and crowns of all teeth simple, conical, and of similar shape (absence of secondary heterodonty).

Type genus: *Pomatodelphis* ALLEN, 1921

Comments. All presently recognized members of the Pomatodelphininae are fossil species from the North Atlantic realm or the Northern Hemisphere. All have elongate and dorsoventrally flattened rostra and symphyseal parts of their mandibles, and a transversely flattened zygomatic process of the squamosal with its medial side concave. *Prepomatodelphis korneuburgensis* from Austria (Figs. 4–6) is the most primitive and earliest known pomatodelphinine. The phylogenetic analysis presented here (Fig. 9) indicates that *Zarhachis flagellator*, of Middle Miocene age from the western North Atlantic, is sister taxon of *Prepomatodelphis*. *Zarhachis flagellator* differs from *P. korneuburgensis* by being larger, having a thickened supraorbital process of the frontal, an enlarged supraorbital maxillary crest, and a more enlarged and more elevated nuchal crest. Species of *Pomatodelphis* ALLEN, 1921, are known from France, Florida (the late Middle Miocene Agricola Fauna that is derived from the Lower Bone Valley Formation in central Florida), and Alabama (HULBERT & WHITMORE, 2006). In species of the genus *Pomatodelphis* the lateral margin of the maxilla immediately anterior to the antorbital notch is thickened and laterally expanded, and the supraorbital maxillary crest is greatly enlarged and knob-like.

Subfamily Platanistinae (GRAY, 1846) BARNES, 2002

Emended diagnosis of subfamily. A subfamily of the family Platanistidae that includes animals differing from

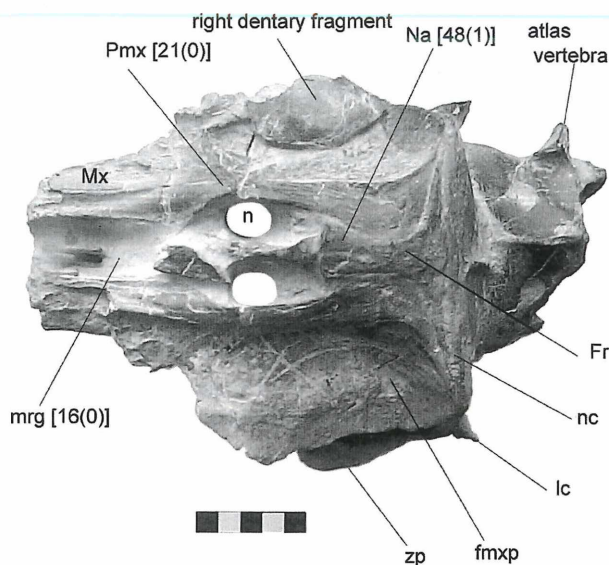


Figure 1: *Allodelphis pratti* WILSON, 1935, holotype cranium in dorsal view, YPM 13408, from the earliest Miocene undifferentiated Freeman Silt and Jewett Sand, near Woody, Kern County, California, U.S.A.; scale bar equals 5 cm; the atlas vertebra remains attached by matrix to the occipital condyles, and a fragment of the posterior part of the right dentary adheres to the dorsal surface of the right supraorbital process. Anatomical abbreviations are explained in Material and Methods.

the Pomatodelphininae by having cranium with transversely (rather than dorsoventrally) flattened rostrum, posterior end of premaxilla narrow and tapered (not expanded transversely), enlarged and anteriorly extended zygomatic process of squamosal, atrophied eye, reduced nasal bones, greatly enlarged supraorbital maxillary crests (which in *Platanista* are fenestrated by extensions from the middle ear air sinus system), reduced lambdoidal crests, secondarily thickened zygomatic process of the jugal; transversely flattened symphyseal portion of mandible; and secondary heterodonty (crowns of anterior teeth greatly elongated apically, crowns of posterior teeth widened transversely).

Type genus: *Platanista* WAGLER, 1830

Comments. *Platanista* is the only genus now included in the subfamily Platanistinae. Its living members are among the most highly derived odontocetes ever to have existed. The reduced size of the bony orbit and the modification of the zygomatic process of the jugal reflect the extremely vestigial nature of the eye. (These are also called blind dolphins [e.g. PILLERI, 1975].) Until more primitive fossil species are described, which might have larger and functional eyes, the reduction of the eye of *Platanista* will remain part of the diagnosis of the subfamily.

Around the North Pacific margin, fossils have been found that appear to belong to the subfamily Platanistinae (CROWLEY et al., 1999), but none of these have been named. One of these apparent platanistine fossils, from the Early Miocene Nye Formation on the coast of Oregon, U.S.A., is part of the symphysis of a mandible (Fig. 7, LACM 131112) that is approximately three times the size of the corresponding part of the mandible of *Platanista gangetica*. It includes the posterior parts of both fused dentaries to the

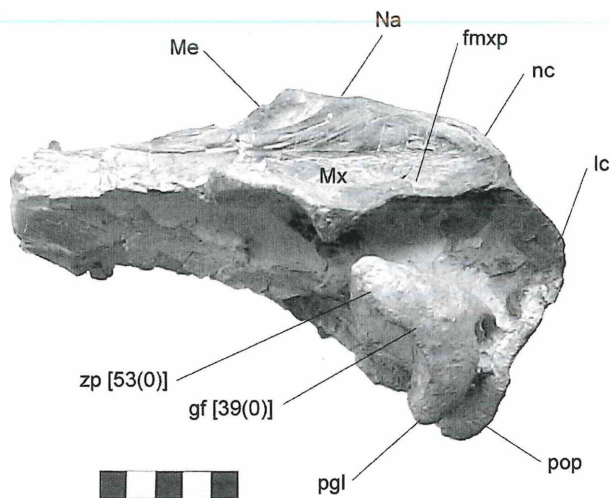


Figure 2: *Allodelphis pratti* WILSON, 1935, holotype cranium in left lateral view, YPM 13408, from the earliest Miocene undifferentiated Freeman Silt and Jewett Sand, near Woody, Kern County, California, U.S.A.; scale bar equals 5 cm; the atlas vertebra has been removed in this image to provide an unobstructed view of the shape of the lambdoidal crest. Anatomical abbreviations are explained in Material and Methods.

anterior-most part of the divergence of the two horizontal rami. It shares with *P. gangetica* transverse compression of the symphysis of the mandible, close approximation of the right and left tooth rows, a longitudinal groove at approximately one-third of the height on the lateral side of the dentary, nutrient foramina positioned dorsal to this groove, and a very slight posterior divergence of the horizontal rami. It differs from *P. gangetica* by being larger, by having a greater separation between the alveolar rows, and by having dental alveoli which at their alveolar rims are round rather than being transversely flattened.

Family Allodelphinidae, new family

Diagnosis of family. A family of the odontocete superfamily Platanistoidea having an elongate and narrow rostrum; premaxillae and maxillae both reaching the anterior rostral extremity; premaxillae and maxillae fused distally; mesorostral groove open dorsally; anteroposteriorly elongated groove present on the lateral side of the rostrum approximately following the maxilla/premaxilla suture; facial region around dorsal narial opening and cranial vertex elevated in the sagittal plane and sloping laterally onto the supraorbital process; posterior maxillary foramen located posterolateral to the external naris and not close to the posterior end of the premaxilla; posterolateral sulcus on premaxilla shallow and not enlarged; posterior end of premaxilla irregular, thin dorsoventrally, and narrow (not expanded transversely); nasal bones elongate anteroposteriorly and narrow transversely; nuchal crest thickened anteroposteriorly and elevated; lateral lamina of the pterygoid present (formed as an outer lamina or bony plate of the pterygoid within the orbit) extending posteriorly from the palate and contacting the falciform process of the squamosal; zygomatic process of squamosal not

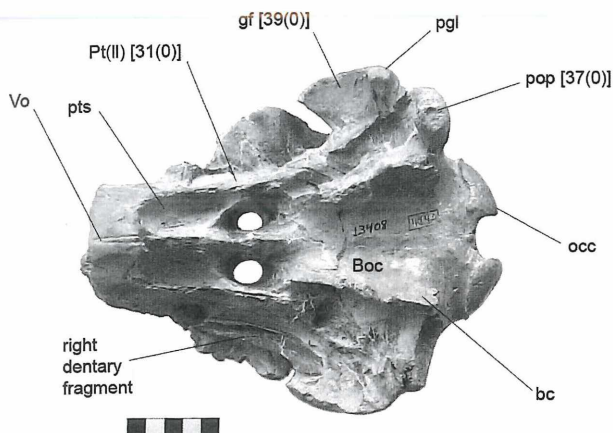


Figure 3: *Allodelphis pratti* WILSON, 1935, holotype cranium in ventral view, YPM 13408, from the earliest Miocene undifferentiated Freeman Silt and Jewett Sand, near Woody, Kern County, California, U.S.A.; scale bar equals 5 cm; the atlas vertebra has been removed in this image to provide an unobstructed view of the shape of the occipital condyles, and a fragment of the posterior part of the right dentary adheres to the ventral surface of the right supraorbital process. Anatomical abbreviations are explained in Material and Methods.

expanded dorsoventrally, not compressed transversely, and glenoid fossa facing anteroventrally; no fossa for posterior sinus present on the anterior surface of the paroccipital process; tympanic bulla with an elongate and pointed anterior spine; tympanic bulla with a thin outer lip that is smoothly overarching and high relative to the transverse width of the bulla; symphyseal portion of mandible narrow and anteroposteriorly elongated, mandibular symphysis firmly ankylosed; and all teeth single-rooted.

Type genus: *Allodelphis* WILSON, 1935

Included taxa and specimens. *Allodelphis pratti* WILSON, 1935, from the earliest Miocene, undifferentiated Freeman Silt and Jewett Sand, Woody Local Fauna, Kern County, California, U.S.A.; a new species that may belong in the genus *Allodelphis* (BARNES et al., 2003; DEERING et al., 2003) from the Early Miocene Vaqueros Formation in Orange County, southern California, U.S.A.; “*Squalodon*” *errabundus* KELLOGG, 1931, from the Middle Miocene Sharktooth Hill Local Fauna, near Bakersfield, Kern County, central California, U.S.A. (see BARNES, 1977: table 3); cf. “*Squalodon*” *errabundus*, of Late Miocene age from southern California, U.S.A. (see BARNES, 1977: table 4).

Distribution. Early through Late Miocene, in the eastern North Pacific Ocean (BARNES, 1977; CROWLEY et al., 1999; BARNES et al., 2003; DEERING et al., 2003).

Comments. BARNES (1977) previously assigned *Allodelphis pratti* and related platanistoids to the family Platanistidae (as did MCKENNA & BELL, 1997). The skulls of allodelphinids superficially resemble those of pomatodelphinine platanistids: both have long rostra, a groove on the lateral side of the rostrum that approximately follows the maxilla/premaxilla suture, and an elongate symphyseal part of the mandible. These characters appear to be convergences. Allodelphinids differ from pomatodelphinines, and all platanistids, by having a primitively constructed zygomatic process of the

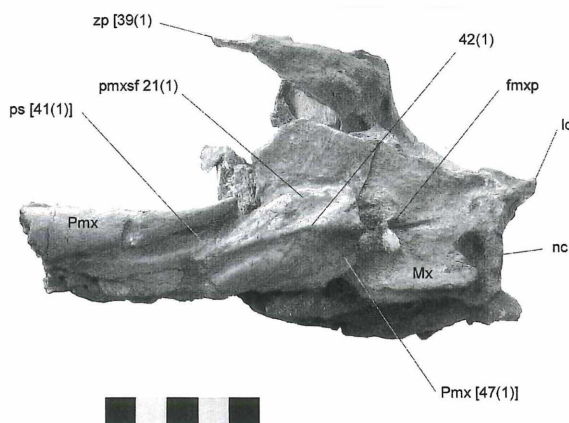


Figure 4: *Prepomatodelphis korneuburgensis* BARNES, 2002, holotype cranium in dorsal view, NHMW 2002z0001/0000, from the latest Early Miocene Korneuburg Formation, Am Teiritzberg, Korneuburg Basin, Austria; scale bar equals 5 cm. Anatomical abbreviations are explained in Material and Methods.

squamosal that is not expanded dorsoventrally, not compressed transversely, and not concave on its medial side, and an anteroventrally-facing glenoid fossa. The posterior end of the premaxilla in allodelphinids is not enlarged and not expanded transversely as it is in pomatodelphinines. Instead, the opposite is the case: in allodelphinids the posterior end of the premaxilla is atrophied: narrow transversely, thin dorsoventrally, and in some specimens irregularly digitated. In allodelphinids, the posterior maxillary foramen is located posterolateral to the dorsal narial opening, and it is separated by a considerable distance from the premaxillary bone (Fig. 1). This is the primitive condition for Odontoceti. The Platanistidae, in contrast, have a derived character state, in which the posterior maxillary foramen is located very close to the posterior end of the premaxilla (Fig. 4).

The perfectly preserved tympanic bulla with the referred specimen of *Allodelphis pratti* (UCMP 83791) has a large anterior spine, such as is present in all species of Platanistoidea. Another *Allodelphis* specimen (USNM 13673) from the same deposit shows that the rostrum and symphyseal part of the mandible are dorsoventrally compressed, that the rostrum has a lateral groove, and that the premaxillae and maxillae are fused distally.

DEERING et al. (2003) and BARNES et al. (2003) reported the discovery of an *Allodelphis*-like platanistoid from the Early Miocene age Vaqueros Formation in Orange County, southern California, U.S.A. That specimen resembles *Allodelphis pratti* by having a long rostrum with a groove on its lateral side along the maxillary/premaxillary suture, a transversely arched facial region across the narial openings and cranial vertex, a prominent and transversely oriented nuchal crest, and a zygomatic process of the squamosal that is of the primitive type: not expanded dorsoventrally and not excavated on its medial surface.

Middle Miocene “*Squalodon*” *errabundus* KELLOGG, 1931, from the Sharktooth Hill Local Fauna in California, was originally named on the basis of isolated petrosals, and was assigned by BARNES (1977) to the family Platanistidae. It is now known by complete crania, mandibles, and as-

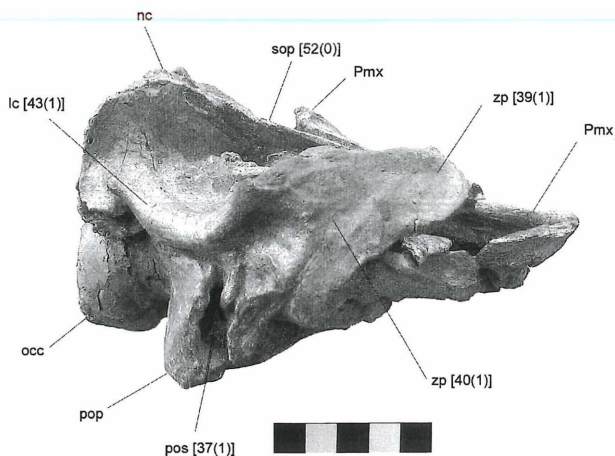


Figure 5: *Prepotatodelphis korneuburgensis* BARNES, 2002, holotype cranium in right lateral view, NHMW 2002z0001/0000, from the latest Early Miocene Korneuburg Formation, Am Teiritzberg, Korneuburg Basin, Austria; scale bar equals 5 cm. Anatomical abbreviations are explained in Material and Methods.

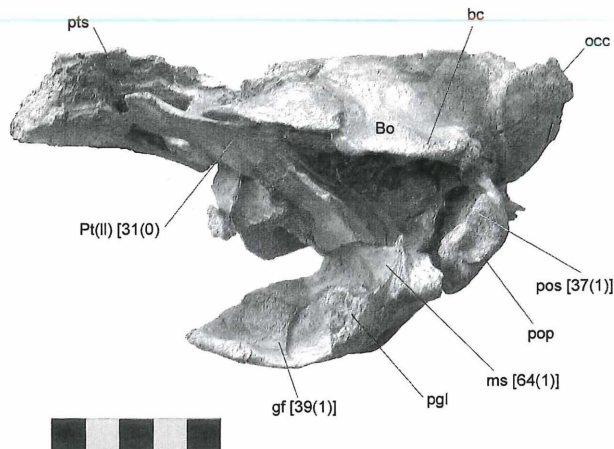


Figure 6: *Prepotatodelphis korneuburgensis* BARNES, 2002, holotype cranium in ventral view, NHMW 2002z0001/0000, from the latest Early Miocene Korneuburg Formation, Am Teiritzberg, Korneuburg Basin, Austria; scale bar equals 5 cm. Anatomical abbreviations are explained in Material and Methods.

sociated petrosals and tympanic bullae (LACM 21258, and 149588), and this species can now confidently be placed in the family Allodelphinidae.

4. Classification

The following classification of the Platanistoidea is derived in part from the classifications that have been proposed by FORDYCE (1994), FORDYCE & BARNES (1994), FORDYCE et al. (1995), and BARNES (2002), and has been modified on the basis of the morphological observations and phylogenetic analysis in this study. This revised classification includes the new family Allodelphinidae, and places that family and the Platanistidae in taxonomic context with the other platanistoids. Parentheses indicate names that originally were proposed by authors at different ranks than they are used here, followed by the name of the reviser, and the date of publication of that revision.

Order Cetacea BRISSON, 1762

Suborder Odontoceti FLOWER, 1864

Superfamily Platanistoidea (GRAY, 1863) SIMPSON, 1945

Family Allodelphinidae, new family

aff. *Allodelphis*, new species, Vaqueros Formation, Early Miocene, southern California

Allodelphis WILSON, 1935

Allodelphis pratti WILSON, 1935

“*Squalodon*” *errabundus* KELLOGG, 1931

Family Squalodontidae BRANDT, 1872

Family Waipatiidae FORDYCE, 1994

Family Squalodelphinidae (DAL PIAZ, 1916) RICE, 1998

Family Platanistidae (GRAY, 1846) GRAY, 1863

Subfamily Pomatodelphininae BARNES, 2002

Prepotatodelphis BARNES, 2002

Prepotatodelphis korneuburgensis BARNES, 2002

Zarhachis COPE, 1868

Zarhachis flagellator COPE, 1868

Pomatodelphis ALLEN, 1921

Pomatodelphis stenorhynchus (HOLL, 1829)

Pomatodelphis inaequalis ALLEN, 1921

Pomatodelphis bobengi (CASE, 1934)

Subfamily Platanistinae (GRAY, 1846) BARNES, 2002

Genus & species undetermined, Nye Formation, Early Miocene, Oregon, U.S.A.

Platanista WAGLER, 1830

Platanista gangetica (ROXBURGH, 1801)

Platanista gangetica gangetica (ROXBURGH, 1801)

Platanista gangetica minor OWEN, 1853

5. Paleocology and paleobiogeography

Pomatodelphininae:

Prepotatodelphis korneuburgensis, of latest Early Miocene age, is the earliest known platanistid, and is from the Central Paratethyan region. All other members of the platanistid subfamily Pomatodelphininae are from the North Atlantic realm. It appears that the Pomatodelphininae originated in the Northern Hemisphere, and possibly in the North Atlantic realm.

The stratigraphic context of the type locality of *Prepotatodelphis korneuburgensis* was provided by SOVIS (1998:34, 36), and the fossil sites at Teiritzberg also are indicated on geologic cross section 4 in figures 2 and 3 of WESSELY (1998:17-18), and in figure 3 of HARZHAUSER et al. (2002). HARZHAUSER et al. (2002: table 1) also listed the co-occurrence of a marine gastropod and a marine bivalve mollusk at the site. The type locality is in the southern part of the paleo-estuary that in Early Miocene time occupied the Korneuburg Basin (HARZHAUSER et al., 2002: figs. 2, 3), which was connected to the larger Vienna Basin. At times the locality where the holotype of *P. korneuburgensis* was discovered had riverine and



Figure 7: Platanistinae, genus and species undetermined, section of the symphysis of mandible, LACM 13112 from LACM locality 5919, Early Miocene, Nye Formation, Lincoln County, Oregon, U.S.A; a, left lateral view; b, occlusal view; and c; anterior view of broken cross section; scale bar equals 5 cm.

estuarine conditions (see HARZHAUSER et al., 2002: fig. 2), but marine conditions prevailed at the time of deposition of the stratigraphically higher part of the deposit that contained the specimen (see HARZHAUSER et al., 2002: fig. 3 [section Teiritzberg 001/I/1990]).

Specimens of *Zarhachis flagellator* are from the Calvert Formation in coastal Maryland, which is part of a well-known sequence of Miocene, marine, muddy inner to middle shelf sediments of the Chesapeake Group that were deposited in the Salisbury Embayment (POAG & WARD, 1993; KIDWELL, 1997). Maximum water depths during deposition of the Chesapeake Group existed during the time of deposition of the Calvert Formation, where planktonic foraminiferal diversity is high, and sharks and other oceanic marine vertebrates are associated with fossils of *Z. flagellator*. Although *Z. flagellator* is from marine deposits, like *Prepomatodelphis korneuburgensis*, it appears to have been living in shallow marine waters near estuarine environments.

Specimens of *Pomatodelphis* from central Florida are from the late Middle Miocene Agricola Fauna, which is derived from the Lower Bone Valley Formation. This fauna includes a mixture of typically oceanic marine vertebrates and terrestrial and fresh water vertebrates (MORGAN, 1994). The pomatodelphinine dolphins of Florida could have been living in either marine or estuarine environments.

HULBERT & WHITMORE (2006) identified a mandible of *Pomatodelphis inaequalis* from a latest Miocene age fresh water deposit in Alabama. This specimen is the geochronologically youngest reported occurrence of a pomatodelphinine platanistid, and it is the only known occurrence of such a dolphin in a strictly fresh water paleoenvironment.

Platanistinae:

The Recent distribution of *Platanista* in south Asia is most closely related to the Pacific Ocean. The occurrence of a mandible of a possible platanistine in the Early Miocene Nye Formation on the Oregon coastline suggests that the origin of the Platanistinae might have been in the North Pacific Ocean, and that the early members of this subfamily were fully marine in their adaptations.

Allodelphinidae:

The earliest known allodelphinid is an un-named dolphin, apparently related to *Allodelphis pratti*, from the Early Miocene Vaqueros Formation in Orange County in southern California (BARNES et al. 2003; DEERING et al., 2003). The Vaqueros Formation is a shallow water, near-shore, marine deposit (MORTON & MILLER, 1981). All of the specimens of *Allodelphis pratti* are from a near-shore but fully marine deposit near Woody, California, (mapped as undifferentiated Freeman Silt and Jewett Sand), where they are found associated with such typical marine vertebrates as sharks, teleost fishes, cetaceans, pinnipeds, and desmostylians (MITCHELL & TEDFORD, 1973; BARNES, 1977). The allodelphinid dolphin known as “*Squalodon*” *errabundus* KELLOGG, 1931, from the marine Sharktooth Hill Bonebed in central California, is part of the rich Sharktooth Hill

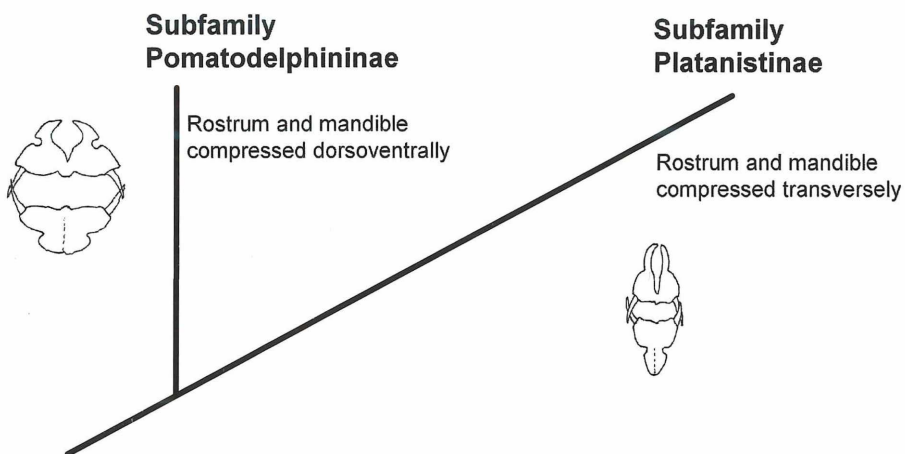


Figure 8: Schematic cross sections of the rostra and mandibles, at approximately mid-length, of representatives of the two different subfamilies of the family Platanistidae. The example for the subfamily Pomatodelphininae is based upon USNM 10485, a referred specimen of Middle Miocene *Zarhachis flagellator* COPE, 1868, from the Calvert Formation in Maryland; the example for the subfamily Platanistinae is based upon CAS 16340, an adult female specimen of Recent *Platanista gangetica* (ROXBURGH, 1801).

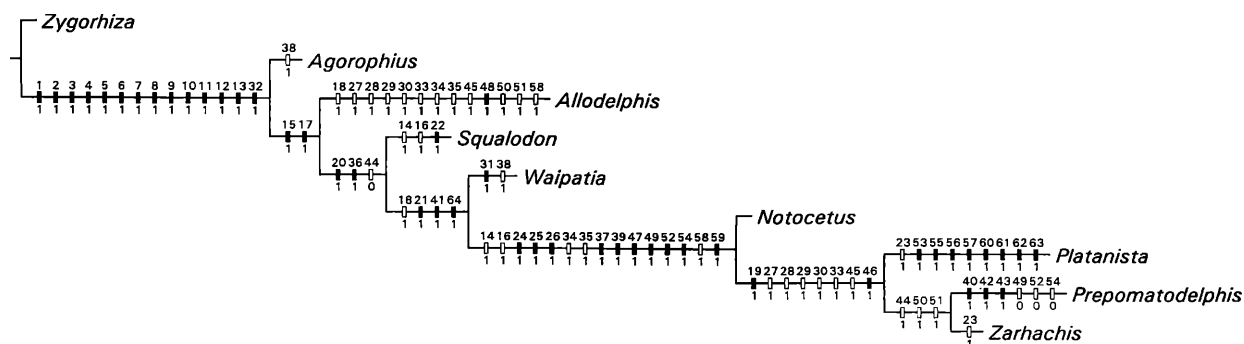


Figure 9: Postulated phylogenetic relationships among nine taxa of fossil Cetacea, including some described members of the superfamily Platanistoidea and of the family Platanistidae, for which reasonably complete crania are available, based on the 64 characters that are explained in Appendix A, using the codings of these characters as they are listed in Table 1. This is the only resulting tree, having a tree length of 84, a Consistency Index of 0.76, a Retention Index of 0.75, and was obtained by manipulating the character matrix (Table 1) with MacClade Version 3.01, and using the Branch and Bound search option of PAUP Version 3.1.1.

Local Fauna of marine vertebrates (MITCHELL & TEDFORD, 1973; BARNES, 1977). It thus appears that the North Pacific allodelphinid dolphins were more fully marine in their adaptations than were the contemporaneous, similar-sized, and equally long-snouted pomatodelphinine dolphins of the North Atlantic realm.

6. Conclusions

1. The family Platanistidae includes dolphin-like odontocete cetaceans, and the family has a known geochronologic range from latest Early Miocene time to the Recent. Its past distribution in Northern Hemisphere marine deposits contrasts with its Recent distribution in south Asian rivers.
2. The described Platanistidae can be classified in two subfamilies: the entirely fossil subfamily Pomatodelphininae, and the fossil and Recent subfamily Platanistinae.
3. The extinct subfamily Pomatodelphininae includes all presently-named fossil Platanistidae: species in the extinct genera *Prepomatodelphis* BARNES, 2002; *Zarhachis* COPE, 1868; and *Pomatodelphis* ALLEN, 1921. These dolphins are latest Early Miocene to latest Miocene in age, and are known only from the North Atlantic realm – from marine deposits in Europe, and the Atlantic and Gulf coasts of eastern North America. *Prepomatodelphis korneuburgensis* BARNES, 2002, from the latest Early Miocene (16.5 Ma to 16.7 Ma, Karpatian stage of Central and western Paratethys, late Burdigalian correlative) Korneuburg Formation in the Korneuburg Basin, Austria, is the most primitive named member of the family Platanistidae, and of the subfamily Pomatodelphininae.
4. The extant subfamily Platanistinae includes comparatively highly derived odontocete taxa: the living genus *Platanista* WAGLER, 1830, which inhabits fresh water in south Asia, and an as-yet unnamed North Pacific fossil species of Early Miocene age from the marine Nye Formation on the coast of Oregon, U.S.A.
5. A phylogenetic analysis demonstrates a basal position among the Platanistoidea for a hitherto poorly known species, *Allodelphis pratti* WILSON, 1935. Accordingly,

the new family Allodelphinidae is proposed for this genus and for some other related species from the North Pacific Ocean. The type genus of this family is *Allodelphis* WILSON, 1935. The type species of *Allodelphis* is *A. pratti* WILSON, 1935, which is known only from Early Miocene marine sediments in central California, U.S.A., identified as undifferentiated Freeman Silt and Jewett Sand. Other species in the family Allodelphinidae are a new taxon related to *Allodelphis pratti* from the Early Miocene Vaqueros Formation in southern California, U.S.A.; and "*Squalodon*" *errabundus* KELLOGG, 1931, from the Middle Miocene (circa 15 Ma) age Sharktooth Hill Bonebed in central California.

6. Most fossils of Pomatodelphininae are from marine sediments, but they are usually found in sediment that was deposited near estuaries or embayments, and one occurrence was in a fresh water deposit. Fossils of Platanistinae and Allodelphinidae are from fully marine environments. The present fresh water environment of *Platanista gangetica*, the only surviving platanistoid, is a relict distribution.

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Characters

Taxon	1	10	11	20	21	30	31	40
<i>Zygorhiza</i>	00000	00000	000-0	-0000	-0000	00000	00000	00000
<i>Agorophius</i>	11?11	11111	11100	00000	0?000	00??0	??0?0	00100
<i>Squalodon</i>	11111	11111	11111	11001	01000	00000	01000	10000
<i>Waipatia</i>	11111	11111	11101	01101	10000	00000	11000	10100
<i>Allodelphis</i>	11111	11111	11101	01100	00000	01111	01111	00000
<i>Notocetus</i>	11111	11111	11111	11101	10011	10000	01011	11010
<i>Prepomatodelphis</i>	11111	11111	111?1	111??	100??	?1111	0?111	11011
<i>Zarhachis</i>	11111	11111	11111	11111	10111	11111	01111	11010
<i>Platanista</i>	11111	11111	11111	11111	10111	11111	01111	11010

Characters

Taxon	41	50	51	60	61-64
<i>Zygorhiza</i>	--010	00000	00000	00000	-000
<i>Agorophius</i>	00010	00000	00000	00000	?000
<i>Squalodon</i>	00000	00000	00000	00000	0000
<i>Waipatia</i>	10000	00000	00000	00000	0001
<i>Allodelphis</i>	00011	00101	10000	00100	0000
<i>Notocetus</i>	10000	01010	01010	00110	0001
<i>Prepomatodelphis</i>	1111?	11001	10000	0?110	0001
<i>Zarhachis</i>	10011	11011	11010	00110	0001
<i>Platanista</i>	10001	10010	01111	11111	1111

Table 1: Matrix of coding of characters that were used in the analysis of relationships of taxa in the superfamily Platanistoidea. The 64 characters are listed and explained in previous text. Character codings are: 0, postulated plesiomorphic condition of a character; 1, postulated apomorphic condition of a character; ?, condition of the character is not preserved on available specimens; and -, the character does not exist in the taxon. The latter two indicators are treated the same in PAUP.

Appendix A. Characters used in the phylogenetic analysis

1. Mesorostral groove: absent (0); or present (1). The mesorostral groove is formed dorsal to the vomer bone, and is flanked on either side by the premaxillae (see ROMMEL, 1990: fig. 2). In life the groove holds the anteroposteriorly elongated mesethmoid cartilage. In some derived species of Odontoceti, notably some species of the family Ziphiidae, the groove is occupied by a mesorostral ossification. The mesorostral groove occurs in no species of the Archaeoceti, and the structure is characteristic of the Mysticeti and Odontoceti.
2. Lacrimal foramen (or groove): present (0); or absent (1). (See GEISLER & SANDERS, 2003:102, character 52).
3. Zygomatic portion of jugal bone thick both dorsoventrally and transversely, as in terrestrial mammals and in the Archaeoceti (0); or narrow, thin, and rod-like (1). (MILLER, 1923; and GEISLER & SANDERS, 2003:102, character 56.) The zygomatic arch of the jugal may be secondarily modified, as in character 61 described below.
4. Dorsal infraorbital foramen (anterior maxillary foramina for cranial nerve V2): having a single dorsal aperture (0); or having multiple dorsal apertures (1). (GEISLER & SANDERS, 2003:103, character 64; illustrated by ROMMEL, 1990: fig. 2.)
5. Lacrimal and jugal: separate bones (0); or fused (1). (See MILLER, 1923; HEYNING, 1989; BARNES, 1990:21, node 10; and GEISLER & SANDERS, 2003:102, character 53.)
6. Antorbital notch: absent (0); or present (1). The antorbital notch is formed between the base of the rostrum and the enlarged anterolateral corner of the supraorbital process, and the notch opens anteriorly or anterolaterally. This is a character of all Odontoceti (BARNES, 1990:21, node 10; ROMMEL, 1990: fig. 2; modified from GEISLER & SANDERS, 2003:102, character 49).
7. Ascending (or frontal) process of the maxilla: abuts the anterior edge of the supraorbital process of the frontal (0); or the ascending process of the maxilla to some degree covers the dorsal surface of the supraorbital process of the frontal (1). This is a character of all Odontoceti, and any posterior extension of the maxilla over the dorsal surface of the frontal bone is considered to represent the derived character state. (MILLER, 1923; BARNES, 1990:21, node 10; modified from FORDYCE, 1994:175, character 3; ROMMEL, 1990: figs. 1-2; and GEISLER & SANDERS, 2003:104, character 76).
8. Premaxillary foramen: absent (0); or present (1). The foramen may have two or three apertures in the right premaxilla, and may be absent due to secondary loss on the left side (as in the members of the superfamily Physeteroidea). This is a character of all Odontoceti, and there is usually a single foramen in each premaxilla (BARNES, 1990:21, node 10; modified from GEISLER & SANDERS, 2003:103, character 69).
9. Posterior maxillary foramen: absent (0); or present (1). This is the foramen that carries the posterior branches of the internal maxillary artery and the maxillary division of the infraorbital nerve. This is a character of all Odontoceti (BARNES, 1990; modified from GEISLER & SANDERS, 2003:104, character 75).
10. Premaxillary sac fossa absent (0); or present (1). The premaxillary sac fossa (see ROMMEL, 1990: fig. 2) is formed on the dorsal surface of the posterior part of the premaxilla that is anterolateral to, or adjacent to, each dorsal narial opening, and posterior to the premaxillary foramen. The ventral wall of the premaxillary sac, which is a diverticulum of the narial passage, lies directly upon this smooth and usually flat, and usually oval-shaped part of the premaxilla. This is a character of all Odontoceti (BARNES, 1990:21; and see AU, 2002: fig. 1).
11. Posterolateral sulcus absent (0); or present (1). This sulcus originates from the premaxillary foramen, traverses posterolaterally to the lateral side of the premaxilla, and usually demarcates the anterolateral and lateral sides of the premaxillary sac fossa (BARNES, 1978:13; modified from MUIZON, 1988b; and GEISLER & SANDERS, 2003:104, character 72).
12. Posteromedial sulcus of premaxilla absent (0); or present (1). This sulcus originates from the premaxillary foramen, traverses posteromedially toward the medial side of the premaxilla, and usually demarcates the anteromedial edge of the premaxillary sac fossa (BARNES, 1978:13).
13. Anteromedial sulcus of premaxilla absent (0); or present (1). This sulcus originates from the premaxillary foramen and traverses anteromedially toward the medial side of the premaxilla (BARNES, 1978:13).
14. Lateral surface of maxilla dorsal to alveolar row and immediately anterior to antorbital notch thickened and expanded laterally to form a flange (0); or lateral margin of maxilla immediately anterior to antorbital notch relatively thin and straight (1). This character is present in Odontoceti only. Most of the earliest-occurring Odontoceti (as exemplified by *Agorophius pygmaeus*) have this lateral expansion of the lateral margin of the maxilla, and it is considered to be a character that is shared among stem Odontoceti. The loss of this lateral flare of the edge of the maxilla among more derived clades of Odontoceti is a derived character state.
15. Maxilla covers anterior part of supraorbital process of frontal and does not contact nuchal crest (0); or extends posteriorly so far as to make contact with the nuchal crest (1). For this analysis, I scored simply whether or not the maxilla reaches the nuchal crest (modified from GEISLER & SANDERS, 2003:104, character 77).
16. Mesorostral groove: open dorsally (0), or roofed over at least in part by the medial margins of the premaxillae (1). The structure is labeled by ROMMEL (1990: fig. 2). The plesiomorphic character state is present in *Agorophius pygmaeus* and in *Allodelphis pratti*, and the derived character state is present in *Zarhachis flagellator* (see KELLOGG, 1924: pl. 1) and *Platanista gangetica* (see VAN BENEDEEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2a, 9a).
17. Right and left parietal bones: make contact along their medial margins on the dorsal surface of the brain case (0); or right and left parietals are separated in dorsal exposure of the cranial surface by posterior extension of maxillae to contact the nuchal crest (1); (see BARNES, 1990:21, node 17).
18. Ascending process of each premaxilla contacts only the lateral side of its respective nasal bone (0); or ascending process of premaxilla extends posteriorly to a point that is posterior to the posterior end of its respective nasal bone (1). The derived character state is shown by the right premaxilla of the speci-

- men of *Zarhachis flagellator* in KELLOGG (1926: pl. 2).
19. Anterior ends of the nasal bones extend anteriorly to overhang, at least to some extent, the posterior side of the dorsal narial openings (0); or nasal bones retracted posteriorly so as not to hang over the posterior side of the dorsal narial openings (1). In the derived character state, the nasal bones do not prevent viewing the entire diameters of the dorsal narial passages in a standard dorsal view of the cranium (for example in *Zarhachis flagellator*, see KELLOGG, 1926: pl. 2).
 20. Nasal bones elongate, having a greater anteroposterior dimension than a transverse dimension (0); or nasal bones shortened and broadened, having lesser anteroposterior dimension than transverse dimension (1). The derived character state exists in *Zarhachis flagellator* (see KELLOGG, 1926: pl. 2).
 21. Premaxillary sac fossae relatively narrow, being approximately the same width as the more anterior parts of the premaxilla anterior to the narial region (0) (as in *Allodelphis pratti*, Fig. 1); or premaxilla wider in the area of the premaxillary sac fossa on either side of the dorsal narial passages (1) (as in *Prepomatodelphis korneuburgensis*, Fig. 4; modified from GEISLER & SANDERS, 2003:98, character 8).
 22. Rostrum narrows in width anteriorly or anterior half of rostrum approximately the same width as the posterior half (0); or anterior end of rostrum widened transversely (1), as in *Squalodon* (see MUIZON, 1991, 1994; GEISLER & SANDERS, 2003:98, character 2).
 23. Anterior end of zygomatic process of squamosal not contacting the postorbital process of the frontal (0); or anterodorsal part of zygomatic process of squamosal having a broad contact with ventral extremity of the postorbital process of frontal (1). The derived character state is present in *Zarhachis flagellator* (see KELLOGG, 1926: pl. 4), and in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2, 9; and FRASER & PURVES, 1960: pls. 17-18).
 24. Posterior ends of right and left maxillae on posterior part of facial region bilaterally symmetrical (0); or posterior end of right maxilla, compared to posterior end of left maxilla, curving farther medially toward the mid-line of the cranium (1). The derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2a, 4, 9a).
 25. Posterior ends of right and left maxillae on posterior part of facial region both of the same height (0); or posterior end of right maxilla, compared to posterior end of left maxilla, having a more concave dorsal surface in the area of the bone that is medial to the temporal fossa (1). The derived character state in some taxa of Odontoceti is associated with the derived state of Character 24, but it is not associated in all taxa. Thus it is regarded here as a separate character. (See VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2a, 9a; and Kellogg 1926: pl. 2.)
 26. Right and left halves of nuchal crest bilaterally symmetrical (0); or left half of nuchal crest, compared to right half of nuchal crest, protruding posteriorly farther than right half of nuchal crest over the dorsal part of the occipital shield (1). The nuchal crest is shown by ROMMEL (1990: fig.2). The derived character state exists in *Platanista gangetica* (VAN BENEDEN & GERVAIS (1868-1880: pl. XXXI, figs. 2a, 9a).
 27. Rostrum not remarkably elongated (0); or rostrum elongated (1). In this study the rostrum is considered to be elongated when it is more than three times the anteroposterior length of the braincase, the latter as measured from the antorbital notches to the occipital condyles (as in *Prepomatodelphis korneuburgensis* [BARNES, 2002: fig. 1] and *Platanista gangetica* [VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs.1, 2, 2a, 2b, 9, 9a; KELLOGG, 1924: pls. 1, 2]).
 28. Premaxillae alone forming rostral extremity (0); or premaxillae and maxillae both reaching the anterior rostral extremity (1).
 29. Premaxillae and maxillae: not fused at distal end of rostrum (0); or fused (1). The derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig.1; modified from FORDYCE, 1994; MESSENGER & MCGUIRE, 1998). In this study I interpret the opposite polarity for the character as was indicated by GEISLER & SANDERS (2003: 99, character 10).
 30. Groove on the lateral side of the rostrum approximately following the maxilla/premaxilla suture: absent (0); or groove present (1). The derived character state is exemplified by *Prepomatodelphis korneuburgensis* (see BARNES, 2002: figs. 1a-b), *Zarhachis flagellator* (see KELLOGG, 1924: pl. 1), and *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig.1), and was defined by FORDYCE (1994: 176, character 36).
 31. Lateral lamina of the pterygoid bone extending posteriorly sufficiently far to contact the alisphenoid bone and/or the falciform process of the squamosal, thus forming an extensive ossified lateral lamina of the pterygoid bone in the ventromedial part of the orbit (0); or lateral lamina of the pterygoid absent (vestigial), not formed as an outer lamina or bony plate of the pterygoid within the orbit, and not extending posteriorly from the palate to contact the alisphenoid and squamosal (1). The primitive character state is present in *Allodelphis pratti* (Fig. 3), *Prepomatodelphis korneuburgensis* (Fig. 6), *Zarhachis flagellator* (see KELLOGG, 1926: pl. 6), and *Platanista gangetica* (see FRASER & PURVES, 1960: pl.18), and was described by FORDYCE (1994:75, character 9). The derived character state is clearly shown in *Steno bredanensis* by FRASER & PURVES (1960: pl. 24).
 32. Anterior end of tympanic bulla rounded (0); or having an elongate and pointed anterior process or spine (1). The derived character state is shown by VAN BENEDEN & GERVAIS (1868-1880: pl. XXXI, figs. 7, 7a, 7b), by KELLOGG (1924: pl. 7, figs. 1-4), and by FRASER & PURVES (1960: pl. 18), and was explained by FORDYCE (1994:176, character 45), and by BARNES (2002:409). Although the petrosal and tympanic bulla are not known for *Prepomatodelphis korneuburgensis*, and other characters of these bones were not included in this analysis, this very distinctive platanistoid character is included here because an anterior bullar spine is present in all known species of Platanistoidea for which the bulla is known, and it undoubtedly was present also in *P. korneuburgensis*, although it was scored as missing data in this study.
 33. Symphyseal portion of mandible not greatly anteroposteriorly elongated (0); or symphyseal portion of mandible anteroposteriorly extended (1). The symphyseal portion of the mandible is considered to be elongated in Cetacea when it is more than one-half of the total length of the mandible (for example in

- Platanista gangetica* [VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig. 3], and in *Zarhachis flagellator* [KELLOGG, 1924: pl. 3]).
34. Mandibular symphysis: unfused (0); or firmly ankylosed (1), (as shown in *Zarhachis flagellator* [KELLOGG, 1924: pl. 3]; and described by FORDYCE [1994:175, character 5]).
 35. Cheek teeth posterior to the first premolar having at least two roots (0), or all premolars and molars single-rooted (1). The homologies of the heterodont dentitions of primitive Cetacea are clearly demonstrated by the Archaeoceti (see KELLOGG, 1936: figs. 30, 31a), and the canine tooth, as is typical for Mammalia, is the first tooth that is rooted in the maxilla. The tooth following the P1 in the Archaeoceti is a single-rooted tooth, or in some taxa a double-rooted tooth. It is considered that a single-rooted P1 (and also the p1) is the plesiomorphic character state for Cetacea. In all Archaeoceti, the P2 (and p2) are two-rooted teeth (see KELLOGG, 1936: fig. 31a), and the presence of single-rooted second premolars, and subsequent premolars and molars, in other Cetacea is the derived character state, and is a step in the development of homodonty.
 36. Facial surface of cranium: not arched transversely in the area of the dorsal narial openings; may be nearly flat transversely or may be ascending posteriorly (0); or arched transversely across the area of the narial openings and the cranial vertex, and sloping laterally onto the supraorbital process (1). The derived character state is present in *Allodelphis pratti* (Figures 1 and 2 herein).
 37. Fossa in the anterior side of the paroccipital process marking the presence in life of a posterior sinus of the middle ear sinus system; absent (0) (as in *Allodelphis pratti* [Fig. 3]); or present (1) (as in *Prepomatodelphis korneuburgensis* [Fig. 6]). The fossa for this sinus is also present in various genera of Odontoceti as shown by FRASER & PURVES (1960: pls. 13 [*Monodon*], 15 [*Delphinapterus*], 17 [*Platanista*], 19-20 [*Pontoporia*, labeled as *Stenodelphis*], 21-22 [*Inia*], 23 [*Lipotes*], 25 [*Sousa*], 27 [*Phocoena*], 28 [*Neophocaena*, labeled as *Neomeris*], 31 [*Orcinus*], 32 [*Orcaella*], 34 [*Globicephala*], 35 [*Feresa*], 36 [*Cephalorhynchus*], 38-40 [*Lagenorhynchus*], 42 [*Grampus*], 44 [*Tursiops*], 45 [*Stenella*], and 47 [*Delphinus*]).
 38. Posterior-most termination of premaxilla with an entire, or rounded margin (0); or posterior termination of premaxilla bifurcated, with the bifurcation containing an exposed wedge of the maxilla (1). The derived character state exists in *Zarhachis flagellator*, as shown by KELLOGG (1926: pl. 2).
 39. Zygomatic process of squamosal: with glenoid fossa facing anteroventrally, and not dorsoventrally expanded on its lateral side (0) (as in *Allodelphis pratti*, see Figs. 2 and 3); or zygomatic process much expanded dorsoventrally, so that its lateral part is thinned transversely, the glenoid fossa is concave medially and closed on its lateral side, and the area of the zygomatic process that is anterior to the glenoid fossa has a medially-directed concavity (1). The derived character state is present in *Prepomatodelphis korneuburgensis* (see BARNES, 2002:415, fig. 2b; and Figs. 4, 5, and 6 herein), in *Zarhachis flagellator* (see KELLOGG, 1926: pl. 5), and in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig. 2b; KELLOGG, 1924: pl. 6; and FRASER & PURVES, 1960: pls. 17-18).
 40. Zygomatic process of squamosal: in lateral view not markedly deeper at the posterior end, having a nearly equal dorsoventral thickness for most of its full length (0); or posterior part of zygomatic process of squamosal much deepened dorsoventrally in its posterior part (1). The derived character state is present in *Prepomatodelphis korneuburgensis* (see BARNES, 2002: 415, fig. 2b; and Figure 5 herein).
 41. Posterolateral sulcus on premaxilla that emanates from the premaxillary foramen; uniform in depth or shallow throughout its length (0); or sulcus very deep, particularly in its posterior part, where its lateral margin may overhang the sulcus (1) (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXX, fig. 19; KELLOGG, 1926: pl. 2; BARNES, 2002: fig. 2a; and Figure 4 herein).
 42. Surface of premaxillary sac fossa on dorsal surface of posterior part of premaxilla; nearly smooth or only slightly convex (0); or undulating, having in its mid-part a sulcus that is bounded both medially and laterally by ridges of bone, and abruptly sloping ventrally at both its medial and lateral margins (1). The derived character state is present in *Prepomatodelphis korneuburgensis* (see BARNES, 2002: fig. 2a; and Figure 4 herein).
 43. Ventrolateral-most part of lambdoidal crest: narrow and only slightly projecting from lateral surface of braincase (0); or much thickened anteroposteriorly and having a prominent rounded edge, that is at least 10 mm thick around the posterior margin of the temporal fossa and spanning from the dorsal surface of the zygomatic process of the squamosal to the lateral wall of the braincase (1). The derived character state is present in *Prepomatodelphis korneuburgensis* (see BARNES, 2002: fig. 2b; and Figure 5 herein).
 44. Nuchal crest: relatively low, and not elevated significantly above the adjacent bones of the posterior part of the facial region (0); or thickened dorsoventrally and elevated above the adjacent maxillary and frontal bones (1). The derived character state is exemplified by *Zarhachis flagellator* (see KELLOGG, 1926: pls. 1-4).
 45. Crowns of teeth: relatively broad and wide anteroposteriorly at the base, the width at the base of the crown being at least one-half of the crown height (0); or tooth crowns dorsoventrally elongate, slender, with pointed apices, the width at the base of the crown being less than one-third of the crown height (1). The derived character state is exemplified by *Zarhachis flagellator* (see KELLOGG, 1924: pls. 1-3). An exception is the acquisition of secondary heterodonty by *Platanista gangetica* (see character 62 following; see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig. 1).
 46. Roots of teeth: conical, elongate, and implanted nearly straight into the rostrum and the dentary (0); or apices of the roots of teeth expanded anteroposteriorly, and in some taxa curved posteriorly (1) (for example see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig. 1).
 47. Posterior end of premaxilla: relatively narrow and not significantly expanded transversely (0); or posterior end of premaxilla much expanded transversely (1). The derived character state is exemplified by *Prepomatodelphis korneuburgensis* (Figure 4 herein) and by *Zarhachis flagellator* (see KELLOGG, 1926: pl. 2).
 48. Nasal bones, whether elongate or shortened, of typical

- width (0); or nasal bones much narrowed transversely (1). The derived character state is present in *Allodelphis pratti* (Figure 1 herein).
49. Supraorbital maxillary crest: not developed on dorsal surface of supraorbital process (0); or supraorbital crest (approximately anteroposteriorly aligned) present on dorsal surface of the maxilla on the supraorbital process (1) (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXX, fig. 1; pl. XXXI, figs. 2, 2a, 9, 9a; and KELLOGG, 1926: pl. 2).
50. Rostrum cross section: not dorsoventrally flattened (0); or rostrum dorsoventrally flattened so that for at least the proximal two-thirds of its length its transverse width is greater than its dorsoventral height (1). The derived character state is present in such pomatodelphinine platanistids as the species of *Prepomatodelphis*, *Zarhachis*, and *Pomatodelphis* (see Figure 8).
51. Mandible cross section: not dorsoventrally flattened (0); or symphyseal portion of the mandible flattened dorsoventrally so that so that in at least its middle one-half the transverse width is greater than its dorsoventral height (1). This derived character state is present in the pomatodelphinine platanistids, for example the species of *Prepomatodelphis*, *Zarhachis*, and *Pomatodelphis* (see Figure 8). This derived character state could possibly be combined with the preceding character, because in the Platanistidae the two appear to be linked. However, the acquisition of the two characters may have occurred at different times, so they are here listed separately.
52. Supraorbital process not significantly thickened, for example in *Prepomatodelphis korneuburgensis* (0) (see Fig. 5); or supraorbital process dorsoventrally thickened, involving parts of both the maxilla and frontal that are dorsal to the orbit (1) (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2, 9; and KELLOGG, 1926: pl. 4).
53. Anterior end of zygomatic process of the squamosal: not remarkably extended anteriorly (0); or anterior end of zygomatic process of the squamosal extended anteriorly (1). The derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXX, fig. 1; pl. XXXI, figs. 2, 9; KELLOGG, 1924: pl. 6; FRASER & PURVES, 1960: pls. 17-18; and GEISLER & SANDERS, 2003: character 188, fig. 13b).
54. Cranial symmetry/asymmetry: mid-line sutures between the right and left nasal and frontal bones at the cranial vertex aligned with the mid-line sagittal plane of the cranium (0); or mid-line sutures between the nasal and frontal bones and dorsal narial openings skewed asymmetrically to the left side of the mid-line sagittal plane of the cranium (1) (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2a, 4, 9a; and listed by BARNES, 1990:21, at node 13).
55. Rostrum not transversely compressed (0); or rostrum transversely compressed so that for at least the proximal two-thirds of its length its transverse width is less than its dorsoventral height (1). The derived character state is present in *Platanista gangetica* (see Figure 8; and VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI).
56. Symphyseal portion of mandible not transversely compressed (0); or symphyseal portion of mandible transversely compressed so that in at least its middle one-half the transverse width is less than its dorsoventral height (1). The derived character state is present in *Platanista gangetica* (see Figure 8; and VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI), and in a possible platanistine of Early Miocene age from Oregon (Fig. 7c).
57. Size of nasal bones: right and left nasal bones of normal size for an odontocete, the transverse width of each bone being approximately equal to the width of the corresponding dorsal narial opening (0); or nasal bones greatly reduced in size (1). The derived character state is present in *Platanista gangetica*, in which the nasal bones are reduced to small tubercles on the anterodorsal surfaces of the frontal bones posterior to the dorsal narial openings (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, fig. 4).
58. Relationship of falciform process of squamosal bone to petrosal: anterior process of petrosal has little contact with the falciform process (0); or falciform process of squamosal bone is enlarged and extends ventrally to have a wide contact with the dorsal side of the anterior process of the petrosal (1). The falciform process descends from the ventral surface of the squamosal (ROMMEL, 1990: fig. 3). The plesiomorphic character state is present in many species of the superfamily Delphinoidea, for example in the phocoenid *Neophocaena phocaenoides* (see FRASER & PURVES, 1960: pl. 28). The derived character state is present in *Platanista gangetica* (see FRASER & PURVES, 1960: pl. 17).
59. Supraorbital process of the frontal: frontal bone not fenestrated by extensions of the pterygoid sinus (0); or fenestration exists to some extent from the ventral surface of the supraorbital process of the frontal in the area of the infraorbital foramen system (1). This occurs because of expansion of a lobe of the pterygoid air sinus from the postorbital area dorsally into the ventral surface of the supraorbital process of the frontal. In the derived character state, which exists in *Platanista gangetica*, multiple branches of the pterygoid sinus extend dorsally toward the infraorbital foramina and spread via the anterior maxillary foramina onto the dorsal surface of the supraorbital process and into the medial side of the maxillary crest (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXX, figs. 19a, 19b; KELLOGG, 1924: pl. 6; and FRASER & PURVES, 1960: 91, fig. 17a, pls. 17-18).
60. Size of the orbit: eye of normal proportions (0); or eye much atrophied (1). The derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2, 9; KELLOGG, 1924: pl. 5; and FRASER & PURVES, 1960: pls. 17-18).
61. Zygomatic process: the zygomatic process of the jugal is narrow, thin, and rod-like in shape, as is the condition in most odontocetes (0); or zygomatic process of jugal is secondarily thickened and shortened anteroposteriorly (1). This modification is correlated with reduction of the size of the orbit, and the derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2, 6, 9; and FRASER & PURVES, 1960: pl. 18).
62. Secondary heterodonty: crowns of teeth are similar in shape throughout the tooth row, and are simple and conical (0); or crowns of the anterior teeth are greatly elongated apically, and the crowns of the posterior teeth are short and widened transversely. The derived character state is present in *Plata-*

nista gangetica (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXX, fig. 1; pl. XXXI, figs. 1, 2, 2b, 9).

63. Lambdoidal crest on the lateral side of the braincase: along the squamosal-exoccipital suture on the surface of the lateral side of the braincase, dorsal to the zygomatic process of the squamosal, the lambdoidal crest is elevated and discernible (0); or the lambdoidal crest in this area is reduced in size and is barely protruding laterally from the side of the cranium (1). The derived character state is present in *Platanista gangetica* (see VAN BENEDEN & GERVAIS, 1868-1880: pl. XXXI, figs. 2, 2a, 9, 9a; and KELLOGG, 1924: pl. 5).

64. Tympanosquamosal recess, or fossa for middle sinus: no fossa developed for middle sinus (0); or fossa is present (1). This fossa, called the tympano-squamosal recess (FRASER & PURVES, 1960; and see FORDYCE, 1994), is the location in life of the middle sinus (see BARNES, 1990:21, node 10), a branch of the middle ear sinus system, and it lies on the ventral surface of the squamosal bone between the ear region and the medial margin of the glenoid fossa on the ventral surface of the squamosal (see for example FRASER & PURVES, 1960: pls. 17-18, where it is shown on specimens of *Platanista gangetica*).

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